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Notulae malacologicae, XLII. Strobilopsidae (Gastropoda, Pulmonata), a family new to the Villafranchian land snail fauna of Apenninic Italy[1]

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The authors report about the finding of a new species of Strobilopsidae, *Eostrobilops aloisii*, from the Villafranchian of central Italy. The description of the new species is followed by a survey of the present knowledge of Recent and fossil Strobilopsidae and a biogeographical analysis of this family.

Key words: Gastropoda, Pulmonata, Strobilopsidae, *Eostrobilops*, systematics, palaeontology, biogeography, Villafranchian, Italy.

During a recent trip to one of the most famous palaeontological sites of central Italy, the Villafranchian (Late Pliocene-Early Pleistocene) fossil wood of Dunarobba, we collected a rich variety of fossil land snail fauna in the clay encrusting the fossil trunks.

About twenty species have been identified, some of great palaeontological and biogeographical interest. Because of the many difficulties involved in locating literature and material for comparison, in this paper we shall only present one finding: a new species of the Strobilopsidae, a family well known in the European Tertiary but never reported before from the Italian Peninsula.

Eostrobilops aloisii sp. n.
(figs. 1-2)

Description. — Shell very small, trochiform, solid, low conical above, convex below. The spire is formed by 4 $^5/_8$-4 $^7/_8$ convex, very narrow and tightly coiled, whorls, separated by deep sutures. Last whorl distinctly angled at the periphery. The umbilicus, c. $^1/_5$ of the shell's maximum diameter, is narrow and deep and slightly enlarged in its final portion. The aperture is semilunar and oblique and the peristome well thickened and reflexed. The parietal margin of the aperture is covered by an evident and thick parietal callus with two parietal lamellae. These lamellae originate deep

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inside the last whorl, at c. 1/4 of a whorl from the aperture, and often have strongly nodose edges over a variable length. Both the lamellae emerge from the aperture, but the lamella parietalis is more readily visible because its final portion is raised. The lamella interparietalis is absent. Deep within the last whorl at c. 1/4 of a whorl from the aperture, level with where the parietal lamellae originate, there is a very short lamella columellaris and one plica basalis. The latter is short and located in the middle of the palatum.

The protoconch consists of c. 1 1/2 whorls and is completely smooth. The teleoconch whorls, on the other hand, are sculptured with numerous growth lines, more evident above the periphery and near the umbilicus and sometimes crossed by spiral lines. Very small, obliquely disposed, scratch-like grooves cross the growth lines.

The shells are shiny and yellow-cream in colour.

Dimensions: height = 1.4-1.7 mm, maximum diameter = 2.3-2.6 mm.

Typical series. — Holotype and 10 paratypes; the holotype is in the Rijksmuseum van Natuurlijke Histoire, Leiden (The Netherlands) no. 56243, and one paratype each in the Museo di Paleontologia dell'Università di Firenze (Italy) no. IGF 2892 E, the Senckenberg-Museum, Frankfurt am Main (W. Germany) no. 307500. Other paratypes and numerous shell fragments in Giusti and Manganelli collection (University of Siena, Italy).

Collection site. — Fornace Briziarelli, Dunarobba (Avigliano Umbro, Perugia) (Sheet 130, "Orvieto", of the geological map of Italy). The shells have been found in the clay encrusting the fossil trunks. There is no general agreement on the age of the layer. Jacobacci et al. (1970) assigned it to the "series of lacustrine clays and sites with lignitiferous beds sometimes with a basal conglomerate" (translated). The lowest portion of this series, containing residues of flora (*Taxodium*, *Nyssa*, *Podocarpus*, *Tsuga*) typical of a warm-temperate climate, is attributed to the Upper Pliocene. Other flora (mainly Taxodiaceae) from the same series in the Todi basin have analogously been attributed to the Lower Villafranchian (upper Pliocene) (Follieri, 1977; Segre, 1986). Ambrosetti et al. (1987, 1989) on the other hand, attributed the trunks of Dunarobba to the Upper Villafranchian (Early Pleistocene) on the basis of typically Pleistocenic fossil species, such as the fresh-water molluscs *Neritina groyana* (Férussac, 1825), *Viviparus belluccii* (De Stefani, 1880), *Melanopsis affinis* Férussac, 1823, *Emmericia umbra* De Stefani, 1877.

Derivatio nominis. — The new species is dedicated to Luigi Manganelli for his help on our collecting expeditions.

Comments. — The new species can clearly be included in the genus *Eostrobilops*. The shell shape, its sculpture, the structure of the apertural armature, the lamellae and plicae originating at c. 1/4 from the aperture, fully agree with what is known about the living and fossil species of *Eostrobilops*.

Eostrobilops aloisii differs not only from the other *Eostrobilops* species, but also from all known Strobilopsidae in having only one plica basalis. Moreover, it is differentiated from *E. diptyx* (O. Boettger, 1869) and *E. boettgeri* (Andreae, 1902) respectively, by a less conical spire and an angled last whorl.

The only other *Eostrobilops* (according to Wenz, 1919) reported from Italy, *Helix* (*Gonostoma*) *patuliformis* Sacco, 1886, differs from the new species because of its more conical shape and only one parietal lamella visible from the aperture. A more careful comparison with the latter species was impossible because of the loss of Sacco's material (see Ferrero Mortara et al., 1984; G. Pavia, personal communication).

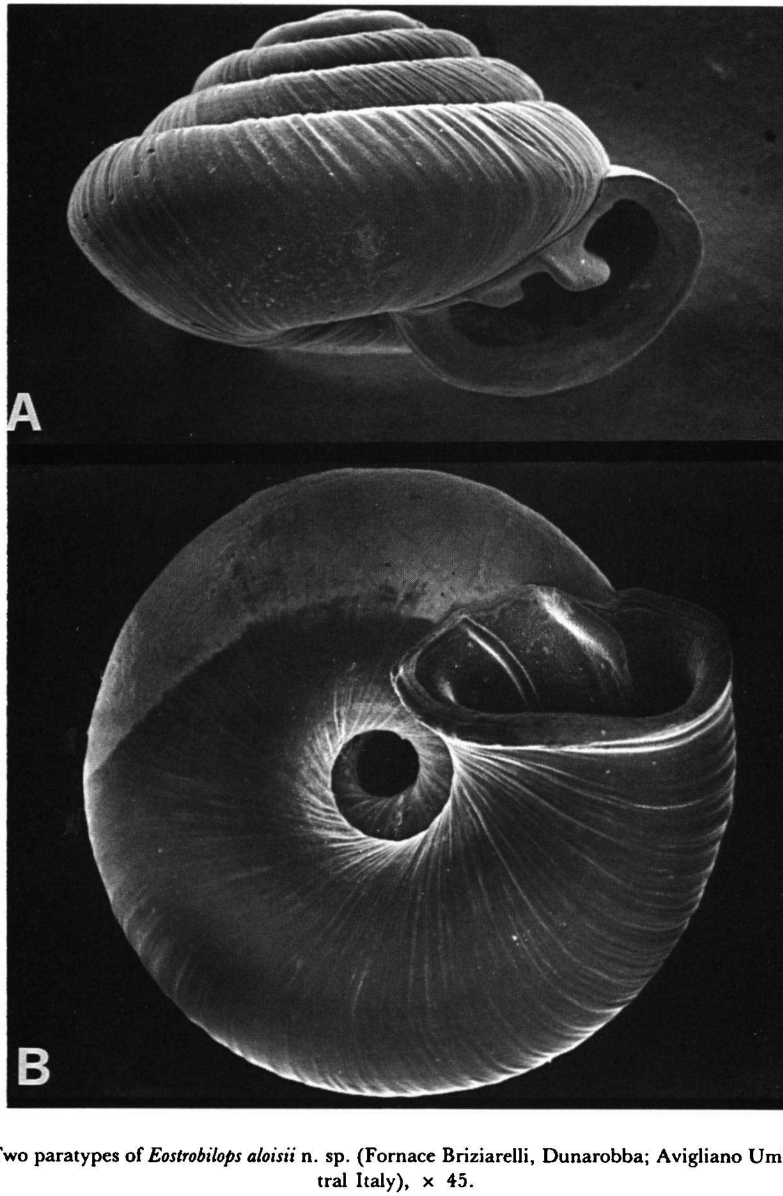


Fig. 1. Two paratypes of *Eostrobilops aloisii* n. sp. (Fornace Briziarelli, Dunarobba; Avigliano Umbro, Central Italy), × 45.

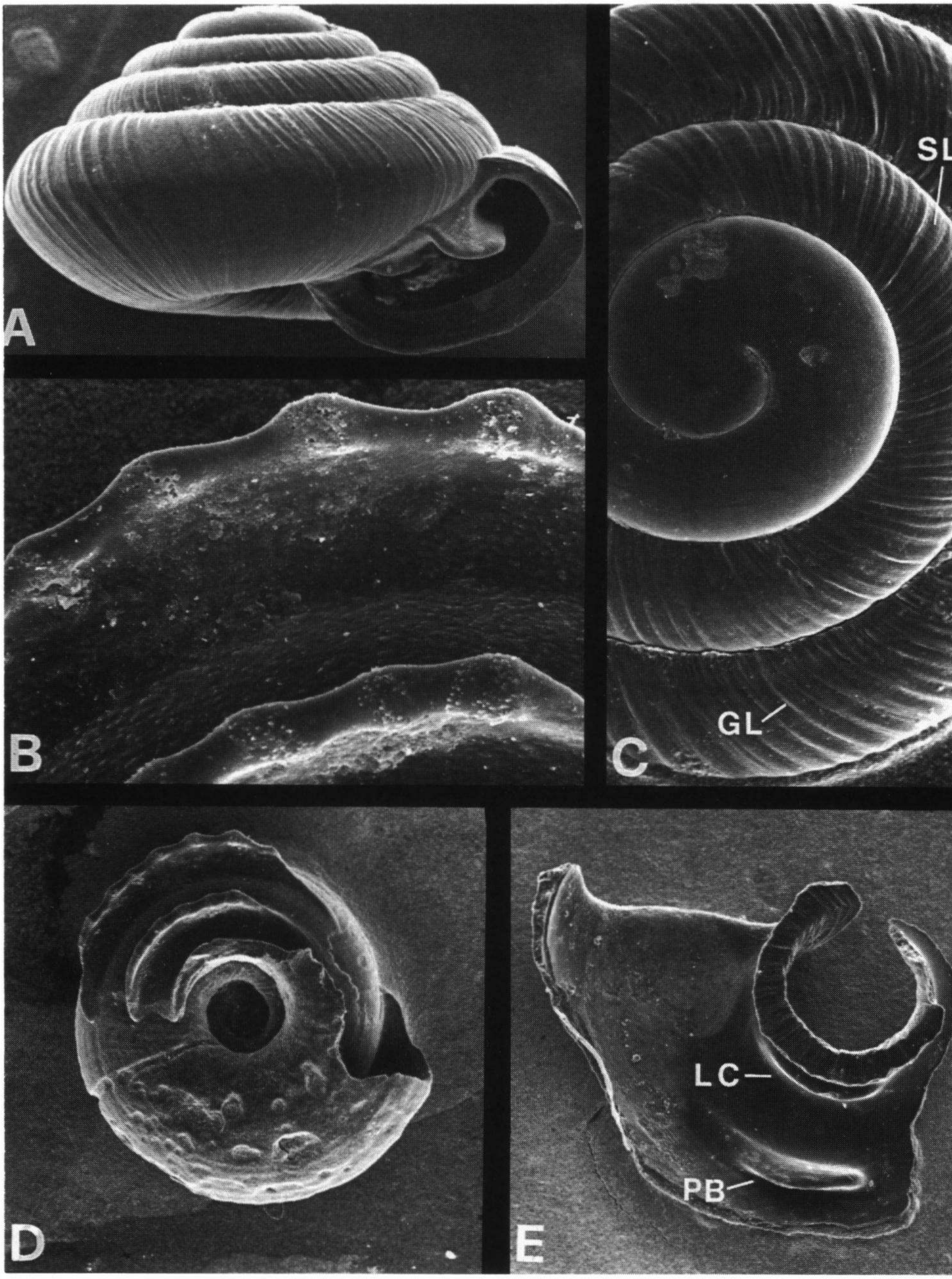


Fig. 2. *Eostrobilops aloisii* n. sp. (Fornace Briziarelli, Dunarobba; Avigliano Umbro, Central Italy). A, Paratype in apertural view. B, Detail of the parietal lamellae. C, Dorsal view of the first whorls; note the growth lines (GL) crossed by spiral lines (SP). D, Umbilical view of a broken shell to show the parietal lamellae. E, detail of the palatum with the lamella columellaris (LC) and the plica basalis (PB). A, D, E ×45; B × 185; C × 90.

No detailed comparison was possible with two supposed *Eostrobilops* known only from very brief and incomplete original descriptions and drawings, "*Pitys*" *dollfusi* Collot, 1911, from the Middle-Upper Miocene of France (Vindobonien, according to Wenz, 1923) and "*Strobilus*" *subconoideus* Jooss, 1912, from the Upper Miocene of Germany (Sarmatian, according to Wenz, 1923). We do not think that this makes it unjustified to describe the present species as new. Any other solution or even the eventual attribution by comparison to one of these two taxa, would be uncertain and negative for a better knowledge of the past history of the group.

An attempt to recognize the ancestral species from which *E. aloisii* originated led to two species, *E. duvali* (Michaud, 1862) from the Middle Pliocene of France (Plaisancien, according to Wenz, 1923) and *E. fischeri* (Wenz, 1914) from the Upper Miocene of Germany (Burdigalien, according to Wenz, 1923), both with similar shell shape and a palatal armature reduced to two small basal plicae. Though older, *E. fischeri* seems closer to *E. aloisii* because of its smaller umbilicus.

BIOGEOGRAPHICAL ANALYSIS

Before starting, we shall give a summary of the present knowledge of the Strobilopsidae.

The living Strobilopsidae. — The Strobilopsidae are a group of orthurethrous Stylommatophora having a wide geographical and stratigraphical distribution. Live species exist in the Americas, China, Japan, the Philippines, and New Guinea, and fossil species date back to the early Tertiary of Europe. The family is exclusively based on the peculiar structure of the last whorl of the shell, as anatomical study has not revealed characters which could distinguish it from other families, such as the Pupillidae or Valloniidae. The systematics of the taxa of the genus and species groups are almost exclusively based on shell characters (shape, sculpture, number of whorls, shape and size of the umbilicus, presence/absence of the lamella interparietalis, presence/absence of the lamella columellaris, number, size and arrangement of the basal and palatal plicae). Only four species belonging to two genera have been studied and described anatomically (Baker in Pilsbry, 1935, 1948; Minato, 1975).

Comprehensive reports on recent Strobilopsidae have been published by Pilsbry (1927-1931, 1948) and Solem (1967).

Pilsbry (1927-1931: 1-63) has furnished the basic data and redescribed all the known species, assigning them to six subgenera or sections of the single genus *Strobilops*: *Strobilops* (s.s.) Pilsbry, 1893 (type-species: *Helix labyrinthica* Say, 1817); *Eostrobilops* Pilsbry, 1927 (type-species: *Strobilops hirasei* Pilsbry, 1908); *Discostrobilops* Pilsbry, 1927 (type-species: *Helix hubbardi* Brown, 1861); *Coelostrobilops* Pilsbry, 1931 (type-species: *Strobilops wenziana* Pilsbry, 1930); *Nesostrobilops* Pilsbry, 1931 (type-species: *Endodonta helleri* Dall, 1900); *Enteroplax* Gude, 1899 (type-species: *Plectopylis quadrasi* Moellendorff, 1893).

Solem (1967) after summarizing all the recent records, revised the oriental genus *Enteroplax*.

In the Americas, 18 species have been reported and assigned to four subgenera: (*Strobilops*, *Discostrobilops*, *Coelostrobilops*, *Nesostrobilops*) (Pilsbry, 1927-1931, 1948; Morrison, 1953; Miller & Christensen, 1980). Twelve of these (some regarded as polytypic), are usually attributed to the nominotypical subgenus. Most live south of

about 52° N and generally east of the 100th meridian. They may be found in northern Mexico, central America, the West Indies and northern South America (Solem, 1967; Miller & Christensen, 1980). Only three species have been studied anatomically [*S. aenea* Pilsbry, 1926, *S. labyrinthica* (Say, 1817), and *S. texasiana* Pilsbry & Ferris, 1906, see Baker in Pilsbry, 1935: 193-195, pl. 26, figs. 4-8; Baker in Pilsbry, 1948: 850-851, fig. 460 4-8]. According to Pilsbry (1927: 19), two groups of species may be identified: "first, that of *S. labyrinthica* (*texasiana* and *affinis* Pilsbry, 1893) in which there are numerous basal plicae and one or two palatal plicae above the periphery; second, the group of *S. strebeli* (L. Pfeiffer, 1862) (*aenea* and the other Mexican and south American species) in which there are 3-4 basal plicae and no palatal plicae". Another species, *S. californica*, recently described by Miller & Christensen (1980) from North Mexico, although referred to *Strobilops* (s.s.) shows some characters, such as a wide umbilicus and only one emerging lamella, which recall the species of the subgenus *Discostrobilops*.

Discostrobilops includes three species known to live in central America: *S. hubbardi* (Brown, 1861) from the coastal plain of the southern U.S.A., north-eastern Mexico, Jamaica, Cuba, Bahama Is.; *S. pilsbryi* Morrison, 1953, from Bermuda Is. (U.S.A.); *S. sinoloa* Morrison, 1953, of which the exact collecting site is unknown, but presumed to be Sinoloa (Mexico). No species of this group has been studied anatomically.

Coelostrobilops includes only two, anatomically unknown species: *S. salvini* (Tristram, 1863) from the mountain forests of Vera Paza (northern Guatemala) and *S. wenziana* Pilsbry, 1930, from Grand Cayman Is. (West Indies).

Nesostrobilops was created for the single species *S. helleri* (Dall, 1900), living in the Galapagos Is.

Recent Asian and New Guinean Strobilopsidae belong to the genera *Eostrobilops* and *Enteroplax*.

One species of *Eostrobilops* has been dissected (Minato, 1975), *E. nipponica* (Pilsbry, 1928); this was found to be very different from the North American species of the genus *Strobilops*. *E. nipponica* has a long diverticulum on the bursa copulatrix duct, totally absent in *Strobilops* (s.s.), no penial appendix or branched retractor penial muscle, and a distal portion of the epiphallus equal in diameter to the proximal portion (in *Strobilops* s.s. the distal epiphallus is very slender and equal in diameter to the vas deferens). *Eostrobilops* includes five species, one polytypic, all known to live in only one or a few sites: *E. diodontina* (Heude, 1880) from Tchen-k'eou (China) (according to Solem, 1967: 24 "probably is Ch'êng-k'ou northeast Ssuch'uon Province = Szechwan, at about 108°47' long., 31°53' lat."); *E. hirasei* (Pilsbry, 1908) from Cheju, Quelpart Island (Korea); *E. nipponica* (Pilsbry, 1928) described from Yonezawa (Japan) and recently also reported from Nagano (Minato, 1975); *E. c. coreana* (Pilsbry, 1920) described from Pyong-Yang (North Korea) and recently also discovered in the Asian Soviet Union (Schileyko, 1984: 155-156); *E. c. echo* (Kuroda & Miyanaga, 1939) from North Korea; *E. kongoensis* (Kuroda & Miyanaga, 1939) from North Korea.

Although anatomically unknown, *Enteroplax* is considered by many recent authors (Zilch, 1960, 1969; Solem, 1967; Habe & Chinen, 1974; Minato, 1975) as a distinct genus. Solem (1967) stated that: "there is a greater morphological gap between the shells of *Enteroplax* and those classified as subgenera or sections of *Strobilops*, than between any of the latter".

Enteroplax appears to include four species: *E. quadrasi* (Moellendorff, 1893) from Luzon, Bohol and Mindanao (Philippine Is.); *E. trochospira* (Moellendorff, 1887) from Cebu (Philippine Is.); *E. polyptychia* (Moellendorff, 1887) from Cebu and Siquijor

(Philippine Is.); *E. misoolensis* (Adam & Van Benthem Jutting, 1939) from Misool Is. (New Guinea).

Another species from Sakishima Is. (Japan) was described as belonging to *Enteroplax* by Habe & Chinen (1974), because of its supposed affinity with species such as *E. trochospira*, *E. quadrasi* and *E. misoolensis* (according to Solem the latter is a junior synonym of *E. quadrasi*).

The fossil Strobilopsidae. — Many fossil taxa have been described in the family Strobilopsidae. Some of them, particularly the most ancient, seem to require more careful study, as their attribution to the Strobilopsidae is obviously difficult to fully establish. Detailed analysis is clearly impossible without a direct study of all material described to date. In what follows we shall try to indicate the reliability of the various data.

The basic data on fossil Strobilopsidae have been discussed and summarized by Wenz (1915, 1923) and Pilsbry (1927-1931). Wenz's (1915) paper was written many years ago when there were far fewer taxa, but is still fundamental because of its good descriptions and the excellent quality of its drawings.

Wenz (1923) lists 26 taxa of the species-group. Since then no less than twenty species and a number of genera have been described from Europe, North America, South America, and China (Baker, 1938; Bartha & Soos, 1955; Steklov, 1961, 1966; Ho & Leonard, 1961; Krumbiegel, 1962; Yen, 1969; Schlickum, 1970; Ferreira & Dos Santos Coelho, 1971; Yü & Wang, 1977; Yü et al., 1982; Yü & Zhang, 1982; Wang, 1982).

According to Wenz (1932) and Krumbiegel (1962) the most ancient records in Europe date back to the Middle Eocene (Upper Lutetian) of Geiseltales (East Germany): *S.* (*Palaeostrobilops*) *carbonaria* Krumbiegel, 1932, *S.* (*Discostrobilops*) spec. and *S.* (*S.*) cf. *joossi* (Gottschick, 1911). Nevertheless, two of these species appear to need careful reconsideration: *S.* (*D.*) spec. (Krumbiegel, 1962: 577; pl. 7, figs. 3a-b) could be interpreted as a species of Discidae; *S.* (*S.*) cf. *joossi* (Krumbiegel 1962: 576-577; table 1; pl. 7, figs. 2a-d) shows a number of lamellae and plicae which does not correspond at all to those of the real *S. joossi*.

Other species are from the Upper Eocene: *S. menardi* (Brongniart, 1810) and *S. monile* (Deshayes, 1863) (according to Wenz, 1923, from the Bartonian of France), *S. gedanensis* (Klebs, 1886) (according to Wenz, 1923, from the Ludien of Bernstein), *S. haedonensis* (Edwards, 1852), *S. pseudolabyrinthica* (Sandberger, 1873), *S. sublabyrinthica* (Edwards, 1852) (according to Wenz, 1923, from the Tongrian of England, France and Germany).

Three of the Eocene species (*S. carbonaria*, *S. menardi*, *S. monile*) were later assigned to the subgenus *Palaeostrobilops* Wenz, 1932 (type-species: *Helix menardi* Brongniart, 1810, subsequent designation; Krumbiegel, 1962: 574). The best known species of the group, *S. menardi*, is characterized by three parietal lamellae, a columellar lamella, five basal plicae, and two long palatal plicae.

Among the remaining taxa, *S. haedonensis* and *S. pseudolabyrinthica* have been thoroughly studied by Cox (1926) and according to Pilsbry (1927) they "approximate rather closely to recent species of the typical *labyrinthica* group". Finally, little is yet known about *S. gedanensis*. *S. sublabyrinthica* was revised by Cox (1926) and recognized to belong to the genus *Acanthinula* (Valloniidae).

According to Wenz (1915, 1919) three different groups of species have originated from this ancestral stock: "Gruppe der *Strobilops diptyx* (BGT)", "Gruppe der

Strobilops costata (SDBR)", "Gruppe der *Strobilops uniplicata* (SDBR)". These groups were considered natural by Pilsbry (1927: 4) and recognized to correspond with some of the taxa of the genus-group introduced by him, the *S. uniplicata*-group in *Discostrobilops*, the *S. costata*-group in the nominotypical subgenus, and the *S. diptyx*-group in *Eostrobilops*.

The first of the above groups, i.e. *Discostrobilops*, includes three taxa: *S. u. uniplicata* (A. Braun in Walchner, 1851), *S. u. plana* (Clessin, 1885) and *S. u. sesquiplicata* (O. Boettger, 1884), all known from Europe, from the Upper Oligocene (Chattian, according to Wenz, 1923) to the Upper Miocene (Tortonian, according to Wenz, 1923).

The second group, i.e. *Strobilops* (s.s.), is very heterogeneous and includes: *S. costata* (Clessin, 1877), *S. joossi* (Gottschick, 1911), *S. labyrinthicula* (Michaud, 1855), *S. romani* (Wenz, 1915), *S. sandbergi* (Lomnicki, 1886), *S. tiarula* (Sandberger, 1886).

The last group, i.e. *Eostrobilops*, includes a sequence of species which substitute each other from the Upper Oligocene (Chattian, according to Wenz, 1923) to the Lower Pliocene (Plaisancien, according to Wenz, 1923): *S. d. diptyx* (O. Boettger, 1869), *S. d. suprema* (Wenz, 1916), *S. fischeri* (Wenz, 1914), *S. dollfusi* (Collot, 1911), *S. boettgeri* (Andreas, 1902), *S. subconoidea* (Jooss, 1912), *S. duvali* (Michaud, 1862). *S. elasmodonta* (Reuss, 1860) has also been proposed for (Wenz, 1915, 1919) or included in (Schlickum, 1970) *Eostrobilops*. According to Wenz (1919), *Helix* (*Gonostoma*) *patuliformis* Sacco, 1886, is another presumed *Eostrobilops*. This species is described from the Villafranchian of Fossano (Piedmont, Italy) and is considered to be the last *Strobilops* of the past European fauna.

More recently described species such as *S. ukrainica* (Steklov, 1966), *S. pachychila* Soos (in Bartha & Soos, 1955) and its junior synonym *S. pappi* Schlickum, 1970, are included in the nominotypical subgenus, while *S. caucasica* Steklov, 1961, and *S. senckenbergi* Schlickum, 1970, belong to the subgenus *Eostrobilops*. *S. senckenbergi* and perhaps also *Helix labassetieri* De Morgan, 1920 (known only from its original description), seem close to *S. elasmodonta* and are possibly synonyms. A last species, overlooked by Wenz (1915, 1923), *S. desmarestina* (Brongniart, 1810) found in the Upper Oligocene of France, cannot be assigned to any group because it is still little known.

In a series of recent papers Yen (1969), Yü & Wang (1977), Yü et al. (1982), Yü & Zhang (1982), and Wang (1982) described numerous new genera and species of the Late Cretaceous and Early Tertiary of China as belonging to the Strobilopsidae.

Except possibly for "*Eostrobilops*" *sinensis* Yen, 1969, and "*Strobilops*" *multidenticulata* Wang (in Yü et al., 1982), all the other taxa seem insufficiently described or seem to have such a peculiar apertural armature as to be hardly accepted as Strobilopsidae (Charopidae, Endodontidae, etc.?).

Very little data are available on fossil Strobilopsidae from North America. One species, *S.* (s.s.) *sparsicosta* Baker, 1938, is known from the Late Pliocene in the Rexrood formation (Meade County) (Baker, 1938; Taylor, 1966) and another species, *S.* (s.s.) *lonsdalei* Ho & Leonard, 1961, is known respectively from the Wisconsian in terrace deposits in the left bank of White River (Crosly County, Texas) (*S. l. lonsdalei*) and from the Kansan deposit of Meade (Meade County, Texas) (*S. l. kansasiana* Ho & Leonard, 1961) (Ho & Leonard, 1961).

There is only one record from South America in a layer supposed to date back to the Late Cretaceous-Early Palaeocene, in the basin of Sao José of Itaborai (Rio de

Janeiro, Brasil): *S. mauryae* Ferreira & Dos Santos Coelho, 1971. This species is based on incomplete shells and its attribution to the Strobilopsidae of the Recent *S.* (s.s.) *aenea*-group, as hypothesized by its authors, is highly speculative.

The above could be considered an indication that the first Strobilopsidae date back to the Upper Cretaceous-Lower Tertiary (*S. maurye, S. multidenticulata, E. sinensis*) of China and South America. Nevertheless, these records are speculative and not a reliable basis for biogeographical analysis.

Information about the Middle Eocene-Upper Pliocene of Europe and the Late Pliocene of North America is more reliable. European fossil records are plentiful and testify to the radiation of taxa at genus and species level.

Conclusions. — Despite many systematic problems in the family Strobilopsidae due to the scarcity of anatomical data and the question of the relationship to families such as the Pupillidae and Valloniidae, we will devote a few lines to the biogeographical aspects.

Pilsbry (1948: 835) has advanced the hypothesis that Asia was the centre of origin of the family; from here the Strobilopsidae could have dispersed both to Europe and North America via an undated Bering connection.

Solem (1979, 1981) cites the distribution of the Strobilopsidae as one of the most interesting cases of "moved" families, i.e. families now living far from the principal stock of fossil records (Europe). Solem (1979: 285) also states that the Eocene Strobilopsidae moved from Europe at the end of the Pliocene and colonized both eastern Asia and eastern North America, suggesting that Europe was an alternative centre of origin to that proposed by Pilsbry (Asia).

If we reject the hypothesis of Ferreira & Dos Santos Coelho (1971) that South America was the centre of origin and dispersion of the Strobilopsidae and if we ignore the two uncertain fossil records from the Late Cretaceous-Early Tertiary of China (which could eventually confirm Pilsbry's hypothesis), it seems possible that the Strobilopsidae originated in the Upper Cretaceous-Early Tertiary in an area of Laurasia corresponding to present-day Europe before continental drift caused the complete separation of North America from Europe. This would make it easier to explain the modern presence of the Strobilopsidae in eastern North America and their absence from western North America. This hypothesis also seems to be supported by Waldén (1984), who includes the Strobilopsidae among the members of a tropical mollusc fauna which existed on the northern border of the Tethys Ocean in the early stages of the opening of the North Atlantic. Later dispersion phenomena may have caused the Strobilopsidae to reach Central America and finally northern South America and the Galapagos Is. and, also, to reach eastern Asia from Europe.

The only point which can be adduced to criticize the above hypothesis is that the North American fossil Strobilopsidae have only been found in extremely Recent beds dating back not later than the Upper Pliocene (Blancan). This, however, may only be a result of the fact that extensive research on the fossil malacofaunas of eastern North America has not yet been performed.

The significance of our finding relative to the origin of the Italian fauna is that it demonstrates how the Apenninic malacofauna originated in strict continuity with that of Central Europe. This continuity was almost certainly established before the Pleistocene and before glaciations drove the central European faunas south.

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